

# Evolutionary Perspectives on Prospective Cognition

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Niko Tinbergen (1963) described four complementary questions to be asked of any animal's behaviour in order to understand it. Two of the questions seek proximate explanations for behaviour: What are the material causes of behaviour? And how does the behaviour develop within the lifetime of an individual? These are questions of *mechanism* and *ontogeny*, and they are the primary focus of many psychologists and neuroscientists. While other chapters in this volume will explore at length the proximate causes of prospective cognition<sup>1</sup>, we will direct our attention to the other two questions, which concern the ultimate, evolutionary causes of prospection: function and phylogeny.

## Function and phylogeny

Evolutionary explanations for an adaptation must enlighten on two key facts: first, the reproductive advantage that adaptation confers upon an individual animal

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<sup>1</sup> There is a necessary ambiguity in the definition of mental time travel as applied to non-human animals, as some degree of difference between species is expected even were we to find great similarities in the nature of prospective thought. Where we use the term 'prospective mental time travel', we refer to the system described by Suddendorf and Corballis (1997; 2007), which has formed the basis for the majority of subsequent comparative research into the topic. We also employ terms such as 'foresight', 'prospective cognition', and 'future-thinking'. We use these terms interchangeably to refer to the processes necessary to represent a future event. These processes may or may not qualify as truly episodic in nature, but without access to a non-human animal's subjective experience, this seems unknowable. Our neutrality with respect to the experiential aspects of prospective mental time travel should be seen as analogous to that of Clayton and Dickinson (1998) in their definition of 'episodic-like' memory as an analogue of human episodic memory.

('function'); second, the constraints imposed on that adaptation by a species' evolutionary history ('phylogeny'). The first of these is easily understood. A large animal's size allows it to retain heat and to fight off rivals, but also imposes a metabolic cost, which reduces the resources that can be devoted to producing offspring and increases the risk of starvation. Natural selection will favour genes that contribute to a more optimal trade-off between cost and benefit, and future generations will cluster around this optimum. In fact, the trade-off between an adaptation's benefits and its metabolic cost is of central importance in the evolution of any new cognitive capacity. Cognitive processing requires a neural substrate, and big brains are expensive, making up 20-25% of the human body's energy needs (Holliday, 1986; Mink et al., 1981). A '*functional*' explanation of prospective cognition must therefore (i) highlight the increased fitness associated with thinking about the future and (ii) assert that these benefits will at least compensate for the concomitant increase in metabolic requirements.

The second evolutionary question is that of '*phylogeny*' – the constraints imposed by an organism's evolutionary history. Natural selection typically acts upon a species gradually and continually, over many generations. A consequence of this is that an optimal adaptation is unreachable if it requires several generations of reduced fitness first. The canonical example is the vertebrate eye, which has a blind spot where the retinal inputs to the optic nerve converge. Because an eye with a blind spot is better than no eye at all, natural selection can only improve upon the existing eye rather than start from scratch with a blind individual. Consequently, vertebrate eyes have been extensively adapted to a range of ecological demands while retaining the suboptimal blind spot (Land and Nilsson, 2002). Psychological

adaptations like prospective mental time travel should then be evaluated as variations upon what came before. As an example, we have recently argued that continuity in hippocampal function across the Animal Kingdom may have constrained the independent evolution of prospective faculties in mammals and birds (Thom and Clayton, 2014).

To summarise, an attempt to understand the evolutionary origins of prospective mental time travel should elucidate the specific fitness advantages conferred by specific variations in those psychological capacities already present in a species. However, the ascription of an adaptive function to a cognitive faculty like mental time travel depends on our knowledge of that faculty, since we cannot infer a cause without understanding the effect. If we wish to take a comparative approach – relating species differences in cognition to variations in the requirements of the ecological niches these species occupy – we must first know the extent of these species differences in cognition. In the case of prospective mental time travel, the focus of most empirical work has been the extent of the difference between human and the rest of the Animal Kingdom. Put simply: Is prospective mental time travel unique to humans? Answering this proximate, mechanistic question is an essential first step in advancing any ultimate, evolutionary account of mental time travel. It is therefore this question, and how best to answer it, that is the topic of the remainder of this chapter.

### **The null hypothesis**

In setting out to identify non-human animals capable of prospective mental time travel we face a problem: How do we know if an observed behaviour is driven by prospective cognition? Consider food-caching. An animal that stores food with the

intention of retrieving it later would certainly seem to be exhibiting some form of prospective cognition. But it is also plausible that evolution has endowed the animal with a desire to cache food, oblivious to the future benefits of doing so. The task is to identify instances in which an animal acts for the future *with the future in mind*.

Lloyd Morgan's Canon, which has dominated interpretations of animal behaviour in the comparative study of cognition, asserts that *"In no case is an animal activity to be interpreted in terms of higher psychological processes if it can be fairly interpreted in terms of processes which stand lower in the scale of psychological evolution and development"* (Morgan, 1903, p. 59). In the case of food-caching, this means that we should assume the second explanation (oblivious desire to cache) is true unless we have good reason to reject it. Ignoring Morgan's archaic use of 'higher' and 'lower', we can see this as an application of Occam's razor to the evolution of intelligence. It is, however, a flawed one. The correct locus of probability is the generation of mutations responsible for changes in psychological processing, not a subjective assertion of the complexity of the relevant process (though see Sober, 2005, and Fitzpatrick, 2008, for a more detailed discussion of Occam's razor in Morgan's Canon). An apparently simple behavioural rule might require a more improbable series of mutations than a cognitive capacity that we intuit to be more complex.

A second problem for Morgan's Canon comes from the particular aspects of cognition we choose to scour the Animal Kingdom for, and where we choose to look. Comparative psychology is not a comprehensive and dispassionate assay of all possible cognitive faculties in all possible species. Aside from the practical difficulties such an endeavour would prevent, researchers would still be limited by their own

imaginations. We tend to look for those cognitive capacities that we see in ourselves, and that we intuitively believe to be most complex. We also typically look first to our closest relatives, the great apes. This preference is not without foundation; Great apes look more like us than other animals, they have large brains like we do (Jerison, 1973), and exhibit some behaviours that we normally think of as very human, like tool-use (Van Lawick-Goodall, 1970). It is however difficult to see how Occam's razor can apply when we ask whether chimpanzees and bonobos share a particular intellectual faculty with humans. We already know the mutations responsible for the faculty in question have arisen because *we have that faculty*. The question is thus not '*How many mutations were required?*', but '*When did these mutations occur?*' We cannot apply a principle of parsimony to conclude that this faculty first emerged in a recent ancestor of modern humans and not a common ancestor of humans, chimpanzees, and bonobos.

It should be noted that the above criticism only applies in cases of *homology*, in which species share a trait because they both inherited it from a shared ancestor. We infer homology of any shared intelligence between humans and chimpanzees because it is more parsimonious to assume that this intelligence emerged once in a shared ancestor than twice in separate lineages. The latter possibility is one of *convergence*, and the criticism of Morgan's Canon from parsimony would not apply in this case. An example of convergence that we will discuss later in this chapter is that of intelligence, and particularly foresight, in the crow family. Because crows and humans are very distally related, our common ancestor is also the ancestor of all mammals and birds, namely a stem amniote. Unless we believe that all mammals and birds are capable of prospective cognition, we might conclude that a great many

mutations were required to *lose* this faculty in other species. More likely, we would argue that this faculty has evolved independently in crows and humans, and that both have simply converged on the same solution to a problem. In this case, the mutations responsible for prospective capacities must have occurred at least twice if we believe that crows are capable of prospective mental time travel. In the absence of any evidence to the contrary, Morgan's Canon will lead us to the most parsimonious conclusion – crows cannot engage in prospective mental time travel.

It should be apparent from the paragraphs above that Lloyd Morgan's Canon is not a strong foundation for assumptions about intelligence in non-human animals, particularly with respect to our closest evolutionary cousins. It nonetheless reflects three beliefs on which to base our null hypothesis. The first is that cognitive explanations are likely to require a more improbable evolutionary history of mutations than a simpler explanation. This has some validity, though the caveats above should be kept in mind. The second belief is that natural selection will not tolerate the expense of an unnecessarily cognitive solution to a problem. This is justifiable in so far as we associated cognitive processing with energy requirements that impose opportunity costs. However, it should be noted that we have little definitive evidence concerning the metabolic costs of specific cognitive faculties. The third belief is intuitive: that there must be something that is qualitatively different about humans, and that something is likely to be an aspect of our intelligence. This third belief could prove to be incorrect, but is widely held and motivates a great deal of interest in animal cognition. These three beliefs supporting Morgan's Canon are not strongly justifiable, but neither are they obviously wrong. In the absence of a

better alternative, we begin with a null hypothesis that no animal, excepting a human, is capable of prospective mental time travel.

The specific articulation of this principle most often tested is the Bischof-Köhler hypothesis, which states that *“animals other than humans cannot anticipate future needs or drive states, and are therefore bound to a present that is defined by their current motivational state”* (from Suddendorf and Corballis, 1997). Suddendorf and Corballis note in presenting this hypothesis that it retains a degree of ambiguity, relying on a common sense definition of “needs”. The qualification of human uniqueness exemplifies the scepticism of Lloyd Morgan’s Canon in limiting mechanistic explanations of non-human behaviour to present drive states. Falsification of the Bischof-Köhler hypothesis is the current gold standard for claims of prospective cognition in non-human animals.

### **The great apes**

Our closest relatives in the Animal Kingdom are the non-human great apes: orang-utans, gorillas, chimpanzees and bonobos. As we have posited above, the argument for the uniqueness of human intelligence may not rely as surely on phylogenetic parsimony in the case of the Great apes. These animals are therefore the logical starting place for our search.

Suddendorf and Corballis (1997) summarise several anecdotal observations of Great ape behaviour that might indicate a capacity to plan for the future. These include a male chimpanzee following and sleeping near to a female while she is in estrus (Goodall, 1986), and carrying straw from inside to make a warm nest on a cold night (De Waal, 1982). A more recent example comes from Furuvik zoo in Sweden,

where a male chimpanzee had been collecting stones and pieces of concrete and later throwing them at visitors (Osvath, 2009). The collecting behaviour had only been observed in the hours before the zoo opened (so in the absence of visitors to throw at), and the caches of projectiles were always discovered on the shoreline facing the visitors. These observations are intriguing, but their anecdotal nature limits their usefulness. In the absence of controlled experiments it is difficult to draw any concrete conclusions (Suddendorf and Corballis, 2010; though see also Osvath and Karvonen, 2012 for a more systematic exploration of the Furuviik chimpanzee's stone-throwing).

A recent study of apparent route-planning in chimpanzees faces the same criticisms. Janmaat et al. (2014) observed the movements, nesting and feeding behaviors of five female chimpanzees in the wild for 275 days. The subjects travelled to a fruit tree each morning for breakfast, and departed earlier when competition for the fruit was likely to be greater (normally smaller fruit that could also be eaten by other, smaller animals). When the next day's breakfast was to be figs – which were typically depleted very quickly – the subjects also tended to position their nests en route to the breakfast tree. The chimpanzees therefore appeared to plan their routes in order to arrive at the breakfast tree before all the fruit had been eaten. Unlike the previous anecdotes, these observations were made systematically over a long period of time. However, when studying a wild population it is impossible to control for confounds from previous life experience (Thom and Clayton, 2015), and controlled manipulations are required to make unambiguous predictions about an animal's behaviour given differing present and future needs.



Two notable studies in the last decade attempted falsification of the Bischof-Köhler hypothesis in Great apes in a more controlled empirical setting. Both studies focused on selection and transport of tools needed to gain access to a food reward in the future. Mulcahy and Call (2006) tested bonobos and orangutans that had been trained to use a tool to access fruit juice in a testing room. The apes were then given the opportunity to select a suitable tool from an array of unsuitable alternatives, at a time when they were unable to access the apparatus containing the fruit juice. The subjects were then ushered out of the testing room, and only given access after an hour. To successfully acquire the juice therefore, the apes had to select the correct tool, carry it outside, keep it, and return to the testing room with it later. They did so on 40.9% trials, significantly more often than would be expected by chance. This finding was also seen in two subjects tested with a longer delay of 14 hours.

In order to establish that this behavior was carried out *with the future in mind*, Mulcahy and Call included a control experiment in which subjects were rewarded for bringing back the correct tool, but the apparatus was not present and the tool was not actually used. This condition therefore tested acquisition of an arbitrary contingency between bringing back the tool and getting the juice. As the authors predicted, the correct tool was returned reliably less often in this experiment than in the previous experiments when the tool had been used. However, two of the four subjects in this control experiment *never* returned the correct tool, and so had no opportunity to acquire the contingency being assessed. The other two performed similarly to those subjects in the other experiments (Suddendorf, 2006). It is therefore possible that the observed behavior can be attributed to long-delay instrumental conditioning (Cheke and Clayton, 2010), by

which the tool could have become associated with the juice reinforcer, facilitated by spending the delay outside the testing room, reducing interference (Lett, 1975). Furthermore, we know nothing of the subjects' motivational states at the time of testing. This same criticism applies to a more recent attempt to replicate Mulcahy and Call's first experiment (Dufour and Sterck, 2008). The apes could plausibly have experienced a present desire for juice without entertaining any particular expectation of an encounter with the apparatus. In the absence of a clear cost to selecting and keeping the correct tool, we might expect a present desire for juice to drive the observed behavior.

Osvath and Osvath (2008) attempted to overcome this hurdle by introducing a self-control element, in which present and future needs are opposed by design. Two chimpanzees and an orangutan were given the opportunity to select a tool from a tray of alternative items. This tool could be used to access some highly valued fruit soup after a 70-minute delay. Initially, the alternative items were non-functional tools, and all three subjects reliably chose the functional tool. In the second experiment, however, one of the alternative items was a piece of the animal's favourite fruit. The subjects therefore faced a choice between an immediately available piece of fruit, and the prospect of future access to a more valuable fruit reward using the functional tool. All three subjects selected the tool on significantly more than the expected 0% of trials.

A third experiment controlled for the possibility that the functional tool had become a secondary reinforcer via its association with the fruit soup. The subjects were now offered two choices instead of one. The first was between a functional tool and several non-functional alternatives, and the second was between another

functional tool, a piece of fruit, and some non-functional tools. If the tool had previously been preferred to the fruit because it had acquired its own reinforcing properties, then the apes would have been expected to choose the functional tool twice. Instead, each of the subjects selected the fruit in the second choice on every trial. The authors infer from their results that the apes were anticipating their future encounter with the fruit soup and their consequent need for a single functional item. In a final experiment, all subjects showed an above-chance preference for a novel functional tool over some equally novel non-functional alternatives. Osvath and Osvath argue that this final finding indicates that their subjects were pre-experiencing their interaction with the apparatus containing the fruit soup, to identify which tool they would need.

In response to Osvath and Osvath's paper, Suddendorf et al. (2009) issued a commentary urging caution. They note that tool-selection in the second experiment was compared to 0%, not to chance. Osvath (2010) responds that chance is not the correct comparison, because the presence of an attractive alternative (the favourite fruit item) would lead a 'future blind' ape to select the functional tool less often than chance. This argument is plausible, and it is unfortunate it remained untested. A simple control could confirm it using a less attractive fruit alternative, which should result in more choices for the functional tool, and fewer for the fruit (and still none for the non-functional tools). Applying this control the third experiment could also strengthen those findings. Since the value of the fruit is always greater than that of a second functional tool, the apes should behave identically and always choose the fruit.

The claims of Osvath and Osvath however rest primarily on the validity of their third experiment, which purports to control for associative learning. Suddendorf et al. suggest that the apes may have held an expectation of an immediate encounter with the apparatus containing the fruit soup, which motivated their initial choice. This would seem surprising since the subjects were never given the opportunity to use the tool immediately after selection. However, one aspect of the apes' behavior does appear inconsistent with anticipation of future tool-use. Suddendorf et al. note that the researchers were able to retrieve the tool after each testing session. If the apes expected to encounter the fruit soup within a trial based on past experience, why would they not expect to do so in future trials? If they did, we might expect them to guard the functional tool for future use. An alternative to this is that the apes also understood that they would always be offered a new tool, based on past experience. One way to test this would be to provide a food option at *both* choices. Given foresight, the optimal behaviour would be to pick the tool once, guard it between trials, and then benefit from both food rewards and the fruit soup on each subsequent trial.

Finally, Suddendorf and colleagues question whether the paradigm used by Osvath and Osvath is capable of testing the Bischof-Köhler hypothesis. Since it is not clear that desire for the fruit and desire for the fruit soup are 'qualitatively' different motivational states, there may be nothing to dissociate from. This criticism betrays an ambiguity at the heart of the Bischof-Köhler hypothesis in its description of present and future 'needs'. The interpretation of needs as drive states is convenient for empirical work, but is extremely limiting if applied universally. If the apes were indeed pre-experiencing a future encounter with the apparatus containing fruit soup,

would anticipation of the need for the tool not be sufficient to be considered a type of episodic foresight? This problem is also apparent in interpreting other studies of tool transportation (e.g. Mulcahy and Call, 2006); it is not clear whether this behaviour could ever satisfy the Bischof-Köhler hypothesis.

The evidence for planning in great ape tool transport is, while impressive, inconclusive. This is partly attributable to the considerable practical constraints involved when working with these animals. Beyond these constraints however, we are left with a critical polysemy in the Bischof-Köhler hypothesis. The vague meaning of 'needs' is clearly a problem for attempts at falsification. Despite the high degree of uncertainty in interpretation of the research presented so far in this chapter, it is difficult not to be impressed with the apes' behavior. When tested on a tool-transport paradigm similar to that of Mulcahy and Call (2006), long-tailed macaques only learned to select and transport tools following shaping with immediate rewards (Dekleva et al., 2012). Furthermore, this behavior mostly stopped with a longer delay of 20 minutes, while Mulcahy and Call's apes tolerated a 14-hour delay. If the great apes show a greater propensity for future-oriented behavior than some other primates, it is important to determine whether this is due to a greater capacity for foresight. We must therefore consider the evidence for prospective cognition in these other primates.

### **Other primates**

Naqshbandi and Roberts (2006) compared the performance of squirrel monkeys and rats in a test of the Bischof-Köhler hypothesis. The animals were given a series of choices between smaller and larger quantities of thirst-inducing food. During the

task, they had limited access to water, and choosing the smaller food reward resulted in earlier (but still delayed) access to the water. All the animals had a baseline preference for the larger food reward, and the authors predicted that an animal capable of foresight would switch their preference to the smaller food reward as the task progressed. The squirrel monkeys tested did so, but the rats did not, leading the authors to conclude that the squirrel monkeys were anticipating their future thirst and acting accordingly. In a follow up control experiment with water availability matched for the two food rewards, the monkeys preferred the larger reward as they had at baseline. This suggests that the rats had not simply become less attractive by association with thirst.

The findings of Naqshbandi and Roberts are promising, and the competition between hunger and thirst would seem to meet the requirement for present and future motivational states to be 'qualitatively' different. Given the problems associated with small study samples however, it should be noted that only two squirrel monkeys were tested. More recent work attempted to replicate this result in rhesus macaques (Paxton and Hampton, 2009). The macaques were tested using the same paradigm as the squirrel monkeys, but continued to select the larger food reward despite the consequent increase in thirst. The authors made systematic variations to the procedure, and found that the macaques did switch to choosing the smaller food reward when the periods of water deprivation were decreased so that there was a 0-minute delay to the return of water when choosing the smaller amount. The macaques' failure in the original task might therefore be attributable to a failure to learn the contingency between choice and water availability over long delays.

The authors go further, noting that the Bischof-Köhler hypothesis does not state how distant ‘the future’ needs to be. Since their macaques were not thirsty when given the choice involving the 0-minute delay (which took as long as needed for the experimenters to return access to water), they did seem to be anticipating thirst in the very near future and thus “...*technically contradict[ing] the Bischof-Köhler hypothesis*”. The oddity of this should be striking. What is implied is either a capacity for foresight that cannot extend into the future, or a capacity to anticipate future events without the ability to learn to expect those future events. It is difficult to envisage the adaptive utility of either. Indeed, enabling an animal to learn about, and later anticipate, the long-term consequences of its action seems an important advantage of mental time travel. That this is not in any way captured by the Bischof-Köhler hypothesis gives good reason for caution in rejecting out of hand behavior that does not meet this particular criterion.

To summarise, the evidence for prospective mental time travel in a non-human primate is promising, but far from conclusive. There have been no undeniable and replicated falsifications of the Bischof-Köhler hypothesis. This is partly due to practical difficulties inherent research, but also due to ambiguities in the hypothesis itself. In the next section, we consider attempts to challenge the Bischof-Köhler hypothesis in a completely different clade: the corvids.

## **The corvids**

The corvids are a family of songbirds including crows, ravens, and jays. They share several important characteristics with primates which have made them attractive prospects for research into comparative cognition: they have large brains for their

body sizes (Emery and Clayton, 2004; Jerison, 1973), some corvids are capable of using tools (Bird and Emery, 2009; Taylor et al., 2007) and of manufacturing them (Bird and Emery, 2009; Weir and Kacelnik, 2006), and some species appear to demonstrate impressive understanding of social problems (Bugnyar and Heinrich, 2005; Emery and Clayton, 2001; Ostojic et al., 2013; Seed et al., 2008). Because corvids are very distant relatives to humans and other primates, their intelligence is believed to have evolved independently to and in parallel with our own (Emery and Clayton, 2004). Since this is a case of convergent evolution, Morgan's Canon can draw support from phylogenetic parsimony in a way it cannot not when we consider great ape intelligence. Nonetheless, our null hypothesis – the Bischof-Köhler hypothesis – is identical.

The focus of much research into corvid prospective cognition has been a single species: the Western scrub-jay (*Aphelocoma californica*). There are two reasons for this. The first is that scrub-jays naturally engage in a future-oriented behavior suitable for exploration; they cache food for future consumption. The second reason is that scrub-jays find and retrieve their caches using flexible memory recall that has been described as analogous to the retrospective component of human mental time travel – episodic memory (Clayton et al., 2003; Clayton and Dickinson, 1998).

Two studies of scrub-jay caching behaviour purport to demonstrate prospective mental time travel. Raby et al. (2007) describe an experiment in which scrub-jays must 'plan for breakfast' by distributing caches appropriately between two rooms in which they might wake the following morning. Correia et al. (2007)



report a falsification of the Bischof-Köhler hypothesis, in which the birds were presented with opposing desires for present and future.

Raby et al. (2007) report two experiments, which took place in a set of three adjacent cages. In Experiment 1, the scrub-jays were shut each morning into one of the end cages. One cage – the ‘breakfast room’ – contained food; the other – the ‘no breakfast room’ – did not. For the rest of the day, the birds had access to all rooms. Each evening, a caching tray was inserted into each of the two end rooms, but only non-cacheable powdered food was available. After three mornings spent in each of the end cages, the birds were given a caching test in which the evening’s powdered food was replaced with whole (cacheable) pine nuts. The birds cached significantly more pine nuts in the ‘no breakfast room’ than they did in the ‘breakfast room’.

The second experiment was similar to the first, but the ‘breakfast’ and ‘no breakfast’ rooms were replaced by a ‘peanut room’, in which peanuts were available for breakfast, and a ‘kibble room’, in which kibble was available for breakfast. Therefore, specific satiety – consumption dependent devaluation of a particular food type – would have resulted in satiety for peanuts in the peanut cage, and for kibble in the kibble room. At the caching test, the birds preferentially cached peanuts in the kibble room, and kibble in the peanut cage. In other words, they cached what they would want at recovery, and where they would want it.

It has been argued that these results contrast with the predictions of an associative account, according to which the animals would have preferentially cached the foods in the cages already associated with those foods. This argument is derived from the fact that rats (*Rattus norvegicus*) eat more in rooms associated with food (Petrovich *et al.*, 2007), and that scrub-jay caching behaviour is partially

controlled by the motivational system that governs eating (de Kort *et al.*, 2007) – presumed to be relatively similar in birds and rats. However, the observed distribution of caches could also result from a preference to spread stores somewhat evenly. Such a preference would be entirely spatial, and would not entail foresight. We should be wary of post hoc heuristic accounts, since it is possible to end up with an overwhelming accumulation of ‘simple rules’ that look decidedly less simple en masse. Nonetheless, a preference for spreading food stores is plausible because we have reason to think scrub-jays might already possess just such a preference. Scrub-jays are scatter hoarders, unlike rats, which tend to store their caches in one or a few places (Vander Wall, 1990). This difference in storing preference must be underpinned by some psychological disparity. If this psychological disparity is a consequence of a capacity for foresight, then we should expect all scatter hoarders to be capable of foresight, which is a strong claim indeed. Conversely, if this psychological disparity between rats and scrub-jays is not related to foresight, then so might be the difference in observed behaviour in the ‘planning for breakfast’ task. Because of this alternative explanation, the findings presented by Raby *et al.* cannot make a conclusive case for prospective mental time travel in scrub-jays.

Correia *et al.* presented scrub-jays with the opportunity to cache while their present desires were in conflict with the desires they would experience in the future, at retrieval. The birds’ motivational states at caching and retrieval were manipulated by pre-feeding with either peanuts or kibble to induce specific satiety. Half of the birds were pre-fed the same food prior to both caching and recovery (the ‘Same’ group), half were pre-fed different foods (the ‘Different’ group). In the ‘Different’ group this induced a conflict, because scrub-jays typically prefer to cache what they

want to eat right now (Clayton and Dickinson, 1999). On the first trial, when the birds had no knowledge of what their states would be at retrieval, both groups preferentially cached the non-pre-fed food. However, on trials 2 and 3, this pattern was reversed in the 'Different' group but not in the 'Same' group. The authors concluded that the birds in the Different group overcame their current motivational state in order to cache what they would want at retrieval, thus falsifying the Bischof-Köhler hypothesis.

A commentary on Correia et al.'s study produced two main criticisms (Suddendorf and Corballis, 2008). First, the birds in the 'Same' group had been presented with more of the pre-fed food type across the course of the experiment than birds in the 'Different' condition. This is true, but it is unclear why this should have affected the birds' motivational states. All birds in both groups had prior experience of the pre-fed food types from previous studies, and all birds had *ad libitum* access to a range of maintenance food types in between trials. Furthermore, subsequent work with Eurasian jays (*Garrulus glandarius*) – another corvid species – replicated the findings of Correia et al. using a within-subject design that prevents this problem (Cheke and Clayton, 2012).

The second criticism focuses on the use of proportions of food types cached in the analysis, rather than absolute numbers. These proportions were criticised for reflecting a reduction in caching of the pre-fed food, rather than an increase in caching of the non-pre-fed food. In other words, the birds did not appear to anticipate a future need for the non-pre-fed food, but instead to anticipate that they would *not* need the pre-fed food. However, this is precisely the one ought to expect given that they began on trial 1 by caching both food types (Clayton et al., 2008). If

the birds had anticipated that they would want *more* of any food at retrieval they would be wrong! The pre-feeding with one food type before retrieval reduced the value of that food type most, but also reduced the value of all foods through its effect on general satiety. Put in lay terms, knowing that you plan to have savoury leftovers for dinner should stop you from buying yourself more savoury food, not encourage you to buy extra dessert.

The evidence from scrub-jay caching is suggestive of a capacity for representing a future motivational state that differs from that being presently experienced. The findings of Correia et al. (2007) and Cheke and Clayton (2012) particularly appear to contradict the Bischof-Köhler hypothesis. It is not however clear that we can conclude from this that scrub-jays are able to engage in prospective mental time travel. It has been noted that many studies of scrub-jay cognition focus on food-caching, perhaps implying a narrow focus for their abilities that contrasts with the broad range of future experiences that humans can envisage (Suddendorf and Corballis, 2010). However, it is entirely possible that the emphasis on caching is a matter of empirical convenience rather than a cognitive limitation. It could therefore be that scrub-jays are indeed capable of foresight beyond a caching context, but we simply have not tested for it.

Recent work in Eurasian jays hints at an avenue for research into foresight in a non-caching context. Male jays share food with their partners in breeding season, and researchers asked whether they anticipate their partners' desires when doing so (Ostojic et al., 2013). They pre-fed the females on one of two food types in order to induce specific satiety, and then gave the males a choice of food types to share. The males preferentially selected and shared the non-pre-fed food, in accordance with

their partners' motivational states. Importantly, this preference was only seen when the males could observe the pre-feeding, so the females were not just cueing the males' choices behaviourally. Subsequent work suggests that the males' food selection is partially driven by their own motivational state (Ostojic et al., 2014). The birds therefore needed to overcome their own desires in order to act to satiate their partner's desires. Given that the selection of food was necessarily made before sharing, and because the Bischof-Köhler hypothesis does not state how far into the future a 'future need' should be (Paxton and Hampton, 2009), it could be argued that food-sharing does indeed provide evidence of foresight beyond caching.

Whether or not one finds the case of food-sharing convincing as a potential example of prospective cognition, the emphasis on caching in studies of scrub-jay cognition ought not to be surprising, for two reasons. Firstly, scrub-jays devote much of their time, energy, and attention to caching, so that is the most obvious manifestation of their cognitive abilities. Consider the analogous example of tool-use in corvids. New Caledonian crows make and use tools in the wild (Orenstein, 1972), and appear to exhibit understanding of novel physical problems (e.g. Weir and Kacelnik, 2006). Similar behaviour was later reported from laboratory studies with Rooks, which are not natural tool-users (Bird and Emery, 2009). From observations of rooks in the wild, we would never have known that they could learn to manufacture tools, simply because they do not naturally experiment with objects as New Caledonian crows do. In the case of tool-use, the Rook studies were conducted because similar work had already been carried out with New Caledonian crows. In the absence of any unambiguous non-caching demonstrations of episodic foresight in a non-human animal, it is not obvious what form a non-caching paradigm should

take. This leads us to a potentially more troubling concern. The Bischof-Köhler hypothesis is intended as a conservative test of non-human foresight, so there may be instances of behaviour for which foresight might be a plausible explanation, but where competing explanations cannot be ruled out. It is possible that the narrow focus of the Bischof-Köhler hypothesis on anticipation of future needs so restricts the range of behaviours from which prospective cognition can be inferred that caching provides the only conclusive examples. If this is indeed the case, we must consider whether the Bischof-Köhler hypothesis continues to be a useful tool for research into future-oriented behaviour.

### **The Bischof-Köhler hypothesis reconsidered**

We have reviewed a range of studies in primates and corvids that purport to examine foresight. A consistent concern has been whether the behaviour in these studies meets the standards of the Bischof-Köhler hypothesis, namely anticipation of future needs that differ from the animal's present needs. One problem has been the ambiguity of the word 'needs', and whether 'motivational state' is an appropriate proxy. Even when behaviour appears to contradict the Bischof-Köhler hypothesis, such as in the case of the Western scrub-jay, we can still draw very few conclusions about the animal's prospective capacities when compared to our own.

It is instructive to consider application of the Bischof-Köhler hypothesis to our own species. Humans are certainly able to anticipate future needs. As an example, we must know that we will need to eat later in the week when going food shopping. If a holiday is approaching and family are visiting for a large meal, we will buy more food than usual. This is clearly an example of acting for the future *with the future in*

*mind*. Nonetheless, it is not necessarily the case that we dissociate completely from the context of our present motivational state when we engage in this behaviour. Indeed, shopping for food is very much influenced by current hunger (Nisbett and Kanouse, 1969), even though that hunger is a temporary state, unlikely to affect our needs in the coming days. It is furthermore unclear whether the desire for food now and the anticipated desire for food later would be considered ‘qualitatively different’ needs.

What we are left with, then, is a criterion that is neither sufficient nor necessary to indicate prospective mental time travel: one can imagine future events without dissociating from present desires, and act for future needs without pre-experiencing them. The Bischof-Köhler hypothesis has been provided an important focus for comparative research into prospective cognition, and has encapsulated the principles laid out in Morgan’s Canon. However, it has also proven highly restrictive as a null hypothesis. We believe that future research will benefit from the development of new criteria for future-oriented cognition.

### **Continuity and criteria**

The logical starting point for development of a behavioural criterion for prospective cognition is with human mental time travel. Indeed, it is because we recognise the importance of this capacity in many behaviours that seem to be uniquely human that we might ask whether foresight represents a discontinuity between our species and other animals. However, there is a risk that this approach is too modular, and that it would be more beneficial to concentrate on individual processes contributing to foresight, rather than the entire cognitive system.

The mental time travel hypothesis lays out an array of cognitive prerequisites for the mental time travel seen in humans, including mental attribution, meta-representation, and the ability to dissociate oneself from the context of the present (Suddendorf and Corballis, 1997). The evolution of human foresight could be a case of 'punctuated equilibrium' (Gould and Eldredge, 1977), in which these component processes emerged rapidly in the short time since our split from the chimpanzee lineage. What would be left is a cognitive chasm between humans and the rest of the Animal Kingdom; a difference in kind rather than degree. If this is not the case, then we must consider the possibility that these processes emerged gradually, with some degree of continuity between species. Either way, it is important to ask whether the component processes of mental time travel facilitate future-oriented action on their own, or whether they are co-opted for that purpose following the emergence of other components. Put simply, does an incomplete mental time travel system – relative to our own – help an animal to act for the future? Where there is a degree of phylogenetic continuity in the processes required for mental time travel, we must consider how each process contributes to future-oriented action in the species endowed with them. Doing so could allow us to relate species differences to differences in ecological demands, and so shed light on the selective forces that shaped the evolution of our own minds.

Corballis (2013; 2014) argues that continuity in hippocampal processing indicates that species differences in foresight are indeed a matter of degree rather than kind. The hippocampus has been implicated as critical in human prospective mental time travel, from neuroimaging studies (e.g. Addis et al., 2007), and from behavioural research on patients with hippocampal damage (Klein et al., 2002;



Rosenbaum et al., 2005). The hippocampus is also important for spatial processing, containing 'place cells' that fire in response to being in a particular location (O'Keefe and Nadel, 1978). Indeed, it has been argued that a key function of the hippocampus in prospection is to provide a spatial framework for imagined future scenes (Hassabis et al., 2007a; Hassabis et al., 2007b; Hassabis and Maguire, 2007). The evidence for continuity comes from activity in rat hippocampal place cells outside of the spatial context to which they refer (Wilson and McNaughton, 1994). This activity can correspond to routes that had not been previously navigated (Gupta et al., 2010), and even to routes that the animal takes subsequently (Pfeiffer and Foster, 2013). We agree that this activity is at least consistent with some component of foresight, and is a plausible building block for the development of human mental time travel (Thom and Clayton, 2014).

### **Future directions**

It is our belief that comparative research has been excessively focused on fulfillment of a behavioural criterion for foresight. Any such criterion can only ever provide us with an arbitrary cut-off point, with some species being deemed capable and others not. This is both unsatisfactory and uninformative. There will always be those who will view any criterion that admits non-human planning as too lax, as there will be those who view dismissal of some such planning as too strict. A single criterion for prospective mental time travel is unlikely to satisfy neither camp. Indeed, Suddendorf and Corballis (1997; 2007; see also Suddendorf, 2013) present mental time travel as a concoction of various contributory mechanisms. This variety in theory must be reflected in the focus of empirical work.

More importantly however, the single criterion approach cannot actually tell us much about the evolution of cognition. A single criterion necessarily dismisses subtle variations in prospective cognition between species. Small variations in processes that are continuous between species give us the opportunity to ask the evolutionary questions we began this chapter with. We can compare these variations to differences in species' ecologies in order to discern their associated adaptive advantages. Similarly, we can ask whether different starting points in cases of convergent evolution offer different constraints on the subsequent evolution of individual processes. It is these processes that should, in our opinion, be the focus of attention in comparative research into prospective mental time travel. Our suggested approach should take its cues from recent neurobiological work, which has made great strides in elucidating the material causes of episodic foresight.

We finish with an example. A defining feature of mental time travel, when compared with semantic memory and non-episodic planning, is that past and future events are experienced in the mind's eye (e.g. Tulving, 2002; Suddendorf and Corballis, 1997). It has been argued that this feature depends on constructive processes – supported by medial temporal brain areas – that establish a spatial framework for the event (Hassabis and Maguire, 2007). This is consistent with work demonstrating hippocampal activity during episodic recall and prospective simulation of the future (e.g. Addis et al., 2007), and also in imagination of an event without any specified time (Hassabis et al., 2007a). Indeed, patients with hippocampal amnesia appear to show impairments in imagination of spatially coherent scenes, but not of single objects (Hassabis et al., 2007b). The processes underpinning 'scene construction' form a small but vital component of mental time

travel. In order to shed light on their evolutionary history, we need to know how they contribute to planning behaviour across species, as well as any role they play in behaviour that is not obviously connected with mental time travel.

Fortunately for the purposes of comparative research, scene construction has been linked to a measurable behavioural phenomenon: boundary extension. Boundary extension is the phenomenon whereby people typically report seeing more of a scene than they actually did, resulting in a more ‘zoomed out’ view (Intraub and Richardson, 1989). In other words, the boundaries of the scene have been extended beyond their natural limits. The link between boundary extension and hippocampal construction rests on two planks. First, boundary extension has been associated with hippocampal activity during initial exposure to a scene (Chadwick et al., 2013). Secondly, the tendency towards boundary extension in healthy individuals produces a paradoxical advantage to recall in patients with hippocampal amnesia (Mullally et al., 2012). Boundary extension in a ‘match-to-sample’ task might therefore be taken as a useful indicator of ‘scene construction-like’ processes, though oriented to the past rather than the future.

Evidence of this kind should not be taken as evidence that an animal is capable of foresight. As we have argued in this chapter, such binary distinctions are unproductive and potentially misleading. Indeed, the processes responsible for boundary extension might be found in an animal that really cannot think about the future (though we are unlikely to ever know this fact with certainty). The hippocampal activity associated with boundary extension was observed primarily during online perception of a scene, leading the authors to suggest that its function might be to provide predictions about the world outside the subject’s field of view.

This function could be beneficial for navigation, even in the absence of an ability to plan the route ahead. Scene construction-like processes might then have been co-opted to support memory and prospection in some species, but not others.

Our highly speculative account of scene construction-like processes is not intended as a just-so story of the evolution of prospective cognition, but as an illustration of the potential benefits of focusing on processes rather than systems. Identifying variations in these processes and assessing their association with environmental demands could offer insight into the selective pressures that shaped our minds, and could potentially offer scope for inference about ancestral forms of human cognition.

### **Concluding remarks**

We began with Tinbergen's two ultimate questions to be asked of prospective mental time travel – what are the adaptive advantages conferred by a capacity for foresight, and how did our earlier evolutionary history influence the form that capacity takes? As a first step towards answering these questions, it is essential to identify the extent to which other, non-human animals are able to plan for the future with the future in mind.

The Bischof-Köhler hypothesis has been the main null hypothesis in this endeavor, articulating the weakly justifiable preference for 'lower' level explanations over more cognitive accounts of behaviour. Several studies claim to falsify the central tenet of the Bischof-Köhler hypothesis – that non-human animals cannot anticipate their future needs. The most convincing examples are of tool transportation in great apes (Osvath and Osvath, 2008), food selection in squirrel

monkeys (Naqshbandi and Roberts, 2006), and food-caching in corvids (Correia et al., 2007; Cheke and Clayton, 2012). These studies are too few in number to be absolutely conclusive, but they do suggest that it is time to stop saying that non-human animals are 'stuck in the present' (a description that has been applied to some humans with hippocampal amnesia; Wearing, 2005; Corkin, 2013).

Some of the criticisms leveled at comparative studies of prospective cognition appear to come down to limitations in Bischof-Köhler hypothesis itself. While the Bischof-Köhler hypothesis has undoubtedly provided a solid foundation for research in this field, it has also been constricting. Its emphasis on anticipation of future needs as distinct from understanding the affordances of a task seems arbitrary. Determining the means of action can tax our ability to imagine and plan just as identifying our goals can. Similarly, the requirement that present and future rewards be qualitatively distinct is vague, but would seem to exclude, for example, all choices people make about money.

We believe that the problems seen in the Bischof-Köhler hypothesis are inevitable if any single criterion for a particular cognitive faculty is insisted upon. We have instead argued for an approach that focuses on individual component processes of prospective mental time travel, even if those processes do not contribute to planning in the subject animal. It is these processes that will provide the variation needed to make meaningful comparisons across phylogeny, and to answer the ultimate questions about our own capacity for foresight. It is time to start seeing the trees for the wood.

## **Acknowledgements**

We would like to thank Lucy Cheke for her comments on this chapter.

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